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THE OPTIMUM INTRAPULMONARY PRESSURE IN UNDERWATER RESPIRATION

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In self-contained breathing sets, oxygen, or a mixture of oxygen and nitrogen, is rebreathed from a counter-lung (a flexible breathing bag), connected to the subject's mouth or face-mask by flexible tubing. The bag is inflated from gas cylinders carried by the subject. When these sets are worn underwater, the pressure of the water upon the chest wall is counteracted by the pressure exerted by the water on the counter-lung and thence transmitted to the gas space within the lungs. The equalization of pressure within and without the lungs can, however, only be approximate, since the chest of a diver in the erect position is exposed not to a single hydrostatic pressure, but to a pressure which increases from above downwards.

It is well known that helmet divers are sensitive to small variations in the pressure of gas respired. J. S. Haldane (1907) described in detail the sensation resulting from too low a pressure of air in the helmet, and ascribed what he observed to the rigidity of the helmet. Provision is, in fact, made for the helmet diver to adjust pressure within the helmet by means of the helmet exhaust valve. In the counter-lung breathing set, however, the diver has no delicate control of the pressure of gas in his breathing bag, apart from being able to vary the degree of filling of the bag with gas. The pressure of gas delivered to the lungs is thus fixed by the position of the bag in the water with respect to the lungs. It is evident that a breathing bag carried by an erect diver at waist level (high intrapulmonary pressure) imposes a considerable resistance to expiration, and conversely, a bag carried at head level (low intrapulmonary pressure) makes inspiration very difficult.

In the breathing sets normally in use, the counter-lung is carried either on the chest, or on the back or as a ring around the neck, and there are considerable subjective differences in comfort according to the type of bag used. The present investigation was undertaken to discover the optimum position of the breathing bag by defining the permissible limits of pressure variation for respiratory function. It soon became clear that the pressure of respired gas is discriminated

subjectively with remarkable delicacy, and for convenience the pressure of the respired gas, at which breathing was most comfortable, has been termed the 'eupnoeic pressure'. Further experiments were performed to throw light upon the cause of the eupnoeic pressure, and on the effect of deviations from it on the respiration.

Throughout this paper the pressure of the gas respired is referred to as the intrapulmonary pressure. When the intrapulmonary pressure is increased, and exceeds the eupnoeic pressure, it is referred to as high, and is plotted on graphs as positive: similarly, when pressures are less than eupnoeic they are referred to as low or negative. A low pressure therefore refers to a pressure smaller than eupnoeic, or negative, and not to one corresponding to the pressure at low level in the water.

METHODS

Subjects were investigated in the vertical and in the horizontal positions. Vertically, they were immersed at least up to the earhole in a tank 3 m. in depth. Horizontally, they rested at full length on the bottom of a tank in water at a depth of 25–30 cm. When they were supine, the back of the head, the shoulders and the buttocks touched the bottom of the tank; when prone, the face was 3-5 cm. and the upper chest 1-2 cm. from the bottom of the tank, and the lower sternum and abdomen were in contact with it.

The gas breathed was either air, oxygen or mixtures of oxygen, nitrogen and CO_2 . It was always breathed through the mouth, the subject wearing a nose-clip. Work was done in the vertical tank on a pedal ergometer, specially constructed for underwater work. The subjects wore bathing trunks and goggles. The water temperature was kept at 97–100° F., except for some of the work experiments, when it was 85–90° F. The subjects were healthy males of ages 21–50 years. Two of them (C.H.L. and P.J. de C.) were Royal Naval diving instructors, experienced in the use of selfcontained breathing apparatus; the remainder were laboratory workers.

Determinations of eupnoeic pressure

The principle of the method was as follows: The subject, immersed to a known depth, breathed from a Douglas Bag under pressure outside the tank; the pressure in the Douglas Bag was then changed according to the subject's signals until he had chosen the most comfortable pressure, which was noted; alternatively, the subject, while breathing air from the bag at a *constant pressure*, varied his *depth* until he was most comfortable. A typical instance was of a subject who, with his earholes 5 cm. below the surface of the water, found a bag pressure of 12.5 cm. of water to be the most comfortable; thus, the chosen (or eupnoeic pressure), relative to the earholes, was 7.5 cm.

The final form of the apparatus used in our later experiments is shown in Fig. 1.

In all determinations the subjects were instructed to 'bracket' their final choice, i.e. to try pressures too low and too high before choosing finally. As a further safeguard, the pressure a which they started was always varied considerably so that they approached their final pressure both from distinctly high and distinctly low pressures.

The eupnoeic pressure refers to the most comfortable pressure of air breathed relative to the pressure exerted by the surrounding water on the chest. It must therefore be referred to some point on the body, preferably some point whose position, in relation to the chest, is well defined and whose distance from the surface of the water can be measured with convenience. Reference points were chosen as follows:

Vertical position. The earhole was taken as reference point. In the head-up position, the eupnoeic pressure is a pressure greater than that of the water at earhole level, and, unless explicit stated, the eupnoeic pressure always means 'cm. below earhole'. In the head-down position, the eupnoeic pressure is again referred to the earhole, but is now less than that of the water at earhole earhole is the earhole is the earhole is the earhole.

level; it is therefore expressed in 'cm. above the earhole', and the numerical value of eupnoeic pressure will decrease as the pressure required for comfort increases.

Horizontal position. For reference, the plane on which the subject was lying was used, i.e. a plane passing through those points of buttock and shoulder or chest and abdomen in contact with the bottom of the tank. The eupnoeic pressure was always less than the pressure of water at the depth of this plane, so that the eupnoeic pressure always refers to 'cm. above the plane on which the subject lies'.



Fig. 1. Diagram of apparatus used for studying underwater respiration.

Respiration and metabolism

A diagram of the apparatus is given in Fig. 1. It consisted of (a) apparatus to supply gas at the required pressure; (b) dry meter and recording apparatus on the inspiratory side of the subject; (c) apparatus for collecting expired air and an expiratory vent.

(a) Consisted of a spring-loaded balloon-fabric pressure bag connected through a 4-way tube to a source of compressed air, to the adjustable water vent (vent 1 on Fig. 1), to the inspiratory tube, and to a pressure tank enclosing the expiratory collecting bag. The compressed gas was supplied either from cylinders or from a small portable compressor. The pressure of the gas delivered to the subject was measured on the water manometer shown, and varied by less than 1 mm. with quiet respiration, and by not more than 0.5 cm. with the largest tidal airs. The pressure was regulated by the depth of vent 1 between 0 and 30 cm. water, vent 2 being adjusted to an equivalent depth. The flow of gas was such that vent 1 bubbled continuously. Tap 1 enabled the pressure to be cut off, and the inspiratory side opened to room air.

(b) Consisted of a Glover dry meter, which recorded minute volumes and respiration rate on a smoked drum, using an integrating device designed by H. B. Barlow. A thermometer inserted through the tube leading from the meter recorded the temperature of the inspired gas.

(c) Consisted of an expiratory tube leading to tap 3, which normally directed the expired air to the expiratory water vent 2 (this consisted of a brass tube closed at the lower end, with three rows of small holes drilled in the circumference near the closed end). When samples of expired air were required, tap 3 was turned so that the air passed into the expiratory collecting bag (capacity 100 l.) enclosed in the pressure tank. This enabled expired air to be collected, without altering the respiratory pressure, for a period limited by the capacity of the collecting bag. At the end of collection, the expired air was directed again through vent 2, and the collecting bag was emptied via taps 4

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and 5 to outside air, a sample being taken from the tubing between these taps. Finally, the taps were set ready for the next sampling. The samples were collected over mercury, and duplicate analyses made with the Haldane apparatus.

Calculations of the oxygen consumption and carbon dioxide production were made on the usual lines.

The accuracy of these determinations, assuming all errors to be working in the same direction, estimated by partial differentials, was $\pm 7\%$. This estimate applies to the technique only. No special precautions were taken to see that subjects were in the post-absorptive state.

Vital capacity and its components

The apparatus described in the preceding section was used, with the addition of the wet meter and 3-way tap enclosed in a dotted line in Fig. 1. This tap enabled an expiration to be delivered, when desired, through the wet meter. Inspiratory volumes were read directly from the dry meter.

In vital capacity determinations, the subject signalled just before and just after his maximal expiration, enabling the operator to pass that expiration alone through the wet meter. For determining reserve air the subject again signalled just before and after the maximal expiration, and the operator passed that expiration alone through the wet meter. For determining complemental air, the subject again signalled before and after his maximal inspiration, and the volume inspired was read on the dry meter. At least three determinations of each were made, and means were taken.

The residual air was not measured directly, but experiments were made to ascertain if it was changed by immersion. In these, the subject breathed from a Benedict spirometer while alternately out of water and immersed.

Instantaneous respiratory air flow

It was expected that, in view of the considerable subjective effects, the deviations in respiratory pressure studied here would affect the rate of air flow during the respiratory cycle. To test this, a sensitive compensating manometer was connected to the mouthpiece of the breathing circuit, and its deflexion was recorded photographically on moving bromide paper with a constant speed camera. By calibrating the manometer for different rates of air flow through the experimental circuit, a series of deflexion-flow calibration curves were obtained from which the peak rates of inspiratory and expiratory flow of submerged subjects during rest and work could be derived.

RESULTS

Eupnoeic pressure

The sensation by which the eupnoeic pressure is judged is complex and hard to define. Chiefly it is located in the chest, but some subjects state that the feeling of distension or otherwise in the mouth and cheeks is an appreciable factor. With low pressures, there is difficulty of inspiration and a much facilitated expiration, sometimes so much so that expiration has actually to be slowed up deliberately. With high pressures, expiration becomes hard, whereas during inspiration the lungs fill almost effortlessly. The balance struck depends on the subject: some aim for a perfect balance; others aim for a slight positive pressure so that they are certain of having no inspiratory difficulty. Subject are unanimous that expiratory difficulty is preferable to inspiratory difficulty

Vertical position

Resting. Determinations were made on eight subjects, the results bein a shown in Table 1. In addition, thirty-one determinations were made on eac

of two subjects, and the distribution of the results is shown in Fig. 2a, b. It is evident that a reliable value for the eupnoeic pressure of any subject, within a few cm. of the true value, can be obtained by a few determinations.





				E.P.	Standard error	No. of de-
Position		$\mathbf{Subject}$	(cn	n. water)	of mean	terminations
Erect		H.B.B.		6.1	1.05	7
Erect		H.P.M.		$7 \cdot 6$	0.85	10
Erect		G.L.B.		$6 \cdot 3$	$3 \cdot 43$	3
Erect		F.C.M.		10.9	6.37	3
Erect		A.S.		$5 \cdot 29$	0.27	31
Erect		W.P.		5.43	0.21	30
Erect		P.J. de C.		10.8	3.68	4
Erect		C.H.L.		11.5	8.13	2
			Mean	8.73 cm.	± 1.1	
Horizontal	Supine	A.S.		15.0		16
	Supine	P.J. de C.		11.3		2
	Supine	C.H.L.		14.5		7
	Supine	G.L.B.		15.0	·	4
	Supine	J.A.B.G.		16.1		3
	1		Mean	14·2 cm.	± 3.45	
Horizontal	Prone	A.S.		10.5		18
	Prone	C.H.L.		12.3		4
	Prone	G.L.B.		10.0		3
	Prone	J.A.B.G.		13.3		5
			Mean	11.5 cm.	± 3.46	
Horizontal o	on side					
Head straight		P.J. de C.		17.0		4
Head straight		C.H.L.		18.0		3
Head down		P.J. de C.		15.0		4
Head down		C.H.L.		11.0		4

TABLE 1. Eupnoeic pressures

During hyperphoea. In two experiments, the subject rebreathed as long as he could from a 50 l. bag without removal of CO_2 . In the first experiment, with a high oxygen content in the gas breathed, there was 8.3% CO₂ in the gas at

the end of the experiment: in the second, using air, there was $7 \cdot 7 \ \% CO_2$ and $11 \cdot 6 \ \% O_2$ at the end. A considerable hyperphoea resulted, during which the eupnoeic pressure rose from $5 \cdot 0$ to $7 \cdot 3$ cm. in the first experiment, and from $5 \cdot 2$ to $8 \cdot 2$ cm. in the second: a mean increase of $2 \cdot 7$ cm.

Another experiment was done, in which the subject indicated his preferred pressure while doing moderate work on the underwater ergometer. His eupnoeic pressure remained the same as at rest.

In further experiments, the eupnoeic pressure during 5 min. maximal exertion was investigated. As it is impossible to signal during such exertion, the subjects were asked to choose the pressure they wanted, before the work, and were asked at the end how it had suited them. There was considerable variation, but the general conclusion was that the eupnoeic pressure may increase to 15 cm. below the earhole, i.e. a pressure 5–10 cm. greater than at rest.

Effect of respiratory resistance. It appeared possible, if a resistance were introduced into the expiratory or inspiratory side of the breathing circuit, that the subject might change his eupnoeic pressure to compensate for it. Thus, with an expiratory resistance, he might lessen his eupnoeic pressure, so that the increased collapsing of his lungs in expiration would help to overcome it.

Resistance (cm. of water at		Eupnoeic pressure (cm. below ear)			
flow)	Position of resistance	W.D.M.P.	A.S. (1)	A.S. (2)	
$3 \cdot 5$	Absent	4.1	4.5		
	Expiratory	4.7	2.9		
	Inspiratory	6.6	3.9		
	Symmetrical		4.9		
17.0	Absent	$5 \cdot 8$	4.5	$5 \cdot 2$	
	Expiratory,	1.7	1.3	0.8	
	Inspiratory	14.6	$8\cdot 2$	11.2	
	Symmetrical	11.0	$7 \cdot 4$	10.1	

TABLE 2. Effect of respiratory resistance on eupnoeic pressure

Table 2 shows the results obtained with two resistances, one light and one severe. They were placed so as to obstruct inspiration, expiration, or both of these. The table shows that the smaller resistance (such as occurs in most respiratory apparatus) has little effect. With the larger resistance a clear-cut result appeared: when the resistance was on the expiratory side of the circuit, a diminution in eupnoeic pressure occurred: when on the inspiratory side, or when symmetrical (i.e. inspiratory and expiratory), an increase in eupnoeic pressure occurred. It should be noted that these experiments were unpleasan because the subject felt that he was being driven into an uncomfortabl compromise.

Horizontal position

Determinations of eupnoeic pressure were made on five subjects, the results being shown in Table 1. It is notable that departures from eupnoeic pressure are tolerated much better in this position: the subjective appreciation of the eupnoeic pressure nevertheless remains acute. Three positions in the horizontal plane have been investigated (supine, prone and on the side), and, as stated above, the results are expressed in terms of the surface on which the subject was lying.

Supine. The average eupnoeic pressure was $14 \cdot 2 \pm 3 \cdot 4$ cm. above the bottom of the tank.

Prone. The average eupnoeic pressure was 11.5 ± 3.5 cm. above the bottom of the tank.

On the side. The eupnoeic pressure was found to depend on whether the subject held his head straight, or allowed it to sink towards the bottom of the tank. With the head straight the average eupnoeic pressure was 17.5 cm. from the bottom of the tank: with the head down, the average eupnoeic pressure was 13 cm. from the bottom. The breadth of the subjects between the lateral surfaces of the deltoids was approximately 40 cm.

Vertical position head down

Determinations of eupnoeic pressure were made on two subjects while they rested with their heads on the bottom of the tank. Each wore a diving set (Davis Submarine Escape Apparatus) whose escape cock (placed at the bottom of the breathing bag) was closed during most of the time. The pressure in the bag was varied by the subject, either by releasing oxygen into the bag, or by cautiously allowing the gas in the bag to escape through the escape-cock. The pressure of the gas in the bag was measured by a mercury manometer outside the tank, connected to the bag by pressure tubing.

The subjects required pressures corresponding to that of water at levels respectively of 19 and 12.5 cm. above the earhole (in the inverted position).

The subjective effects of varying the respiratory pressure either side of this level were reported as similar to those in the vertical position head up.

Limits of tolerance

An attempt was made in two experiments to determine the maximum tolerable limits of pressure variation. The two subjects were diving instructors. The limits so obtained were, for the two subjects, 34 and 28 cm. greater pressure than eupnoeic, and 22 and 28 cm. less pressure than eupnoeic. The limiting factor on the side of excess pressure was inability to prevent gas escaping round the mouthpiece. With negative pressure there was pain in the lower chest and throat, and in one subject in the right shoulder (possibly 'referred' from diaphragm). The conditions were optimum for tolerating un-

pleasant pressures. Less experienced subjects, longer exposure, or work would undoubtedly have lessened the size of variation tolerable.

The reference planes mentioned so far were chosen as being the most convenient to measure underwater. Measurements of the subject showed, however, that the supra-sternal notch provides a more useful reference point, for in every position the eupnoeic pressure is at the level of the sternal notch, with one exception, viz. the vertical (head-up) position at rest, when the eupnoeic pressure is 5–10 cm. above the notch.

TABLE 3. Difference between vital capacity in air and best immersed vital capacity

	Vital capacity in	
	air minus best	Pressure when
	immersed vital	immersed (cm.
Subject	capacity (l.)	below earhole)
H.B.B.	0.6	27.5
F.C.M.	0.14	28.0
A.S.	0.31	17.9
W.P.	0.68	6.4
C.H.L.	0.02	$25 \cdot 0$
	$Average = \overline{0.35}$	20.9



	Vital capacity in air minus vital capacity	
	at eupnoeic pressure	Eupnoeic pressure
Subject	(l.)	(cm. below earhole)
H.B.B.	1.7	6
F.C.M.	0.5	12
A.S.	0.4	7
W.P.	1.0	6
C.H.L.	0.1	11
	Average = 0.74	8.5

Experiments on the vital capacity

Although these experiments provide objective evidence on the effects of varying intrapulmonary pressure on respiration, much depends on the zeal of the subject; thus, the lessening of vital capacity with relatively low pressures is certainly due in part to the unpleasantness of inspiring deeply under these conditions. Subjects were instructed not to strain themselves, but to make an effort similar to that at more comfortable pressures. The results are shown in Figs. 3 and 4 and in Tables 3 and 4.

There is clearly great variation among individuals, permitting only general conclusions. Immersion vertically in the water diminished the vital capacity at all intrapulmonary pressures. This diminution is less with positive pressures and much greater with negative pressures. But even an increase in pressure sufficient to cause considerable discomfort never restored the vital capacity to a magnitude normal in air. A few experiments on the effects of high and low pressures when the subject was not immersed showed that both these diminished the vital capacity. This suggests that high pressures underwater increase the vital capacity (relative to that at eupnoeic pressure) only by counteracting the surrounding hydrostatic pressure.



Fig. 3. Effects of varying the intrapulmonary pressure on the vital capacity when the subject is immersed vertically.



Fig. 4. Effect of varying the intrapulmonary pressure on the vital capacity when the subject is immersed horizontally.

Experiments with a horizontal position in water showed only a slight diminution in vital capacity at eupnoeic pressure, compared with that in air, and the effects of variation in pressure were small.

Complemental and reserve air. Fig. 5 shows the effect of vertical and horizontal postures and of various intrapulmonary pressures, on these components of the vital capacity. Closely similar results were obtained with other subjects.

In the horizontal position, the reserve and complemental airs are normal at eupnoeic pressure, and the tidal air occupies its normal position in the respiratory range. There is also an increase in reserve air with positive pressure about 1 l. for 15 cm. increase of pressure. A definite, but smaller, decrease occurs with negative pressure.

In the erect position, at eupnoeic pressure, the reserve air is reduced to about 500 c.c. (range 250–700 c.c. in six subjects) and is reduced little further by negative pressures. This probably represents the lowest value it can reach within the limits of tolerable respiration. Strongly positive pressures sometimes restore it to a level normal for breathing when not immersed, but such pressures



Fig. 5. Effect of varying the intrapulmonary pressure on the complemental and reserve airs. (Thick lines refer to horizontal position, with intrapulmonary pressure in cm. above supporting surface. Thin lines refer to vertical position, with intrapulmonary pressure in cm. below ear.)

are distinctly uncomfortable. Thus, for a subject immersed, the most comfortable position of the tidal air in the respiratory range is substantially nearer the limit of expiration than it is when breathing normally in air.

The changes in complemental air are all in the corresponding direction, but reflect also the changes in vital capacity. Less importance can be attached to these results, as it was not found so easy to obtain consistent maximum inspirations as to obtain consistent maximum expirations. The results provide, however, a useful verification of the results for reserve air.

Residual air. Several subjects, breathing from a Benedict spirometer at atmospheric pressure, were studied while out of water and while immersed to 3-5 cm. above the supra-sternal notch. From what had been found regarding the eupnoeic pressure, these conditions when the subject is immersed are closed

to those when he is totally immersed and breathing at eupnoeic pressure. Tracings were taken of normal respiration and maximum expirations while out of water and while immersed alternately. Fig. 6 shows a typical tracing. The shift in tidal position towards expiration, resulting from immersion, is clearly seen.



Fig. 6. Spirometer tracing of respiration and maximum expiration with the subject alternately immersed (*Imm.*), and out of water. The dotted line drawn through the ends of the maximum expirations shows that there is in this subject (C.P.) no significant change in the residual air due to immersion. (Tracing read from right to left.)

To obtain evidence whether there was also any change in residual air on immersion, a line was drawn between the lowest points of the maximum expiration while out of water. This line represents the division between reserve and residual air: on immersion, any deviation of the lowest point of maximum expiration from this line must mean a change in the residual air: if the latter

were diminished, the maximum expiration would pass below the line. Thus, although the absolute value of the residual air was not measured, any relative change in it could be detected.

In experiments on five subjects, the diminution in residual air ranged from zero to 300 c.c., averaging 150 c.c. The tracing shown in Fig. 6 is from a subject in whom immersion caused no significant decrease in residual air.

Pulmonary ventilation underwater

Previous sections have defined the eupnoeic pressure and have shown certain effects of immersion and non-eupnoeic pressures on the vital capacity and its components. It is now necessary to consider the effects of immersion and varying intrapulmonary pressure on the breathing generally.

Oxygen consumption. It is, of course, necessary to know the oxygen consumption in any experiment before the data obtained (such as minute volume or tidal air) can be compared with those under other conditions. All the data obtained have been plotted against oxygen consumption to allow for this variable.

The changes of R.Q. with increasing oxygen consumption normally found in air were also observed in these experiments. The highest oxygen consumptions recorded were about 2 l./min. Variations in intrapulmonary pressure, sufficient to produce considerable discomfort did not cause any detectable increase in oxygen consumption. Any contribution to the oxygen consumption from this cause of respiratory effort was therefore less than 50 c.c./min.

Minute volume. In Fig. 7 are plotted the minute volumes of subjects, z breathing air, for various oxygen consumptions, with intrapulmonary pressures above and below eupnoeic level. Through these are drawn lines, derived from the Handbook of Respiratory Data in Aviation (1944), which show the average rise in minute volume with increasing oxygen consumption during work in air, and the limits which enclose 95% of their results. Two points are clear: (a) that minute volumes of the working immersed subject breathing air are closely similar to those of a subject working in air with the same oxygen consumption; (b) that variations in intrapulmonary pressure do not affect the minute volume. It should be noted, however, that one subject at rest overventilated with non-eupnoeic pressures, during which time his R.Q. was well over 1.0. It is probable that such individual variations would be common in subjects at rest, unused to varying pressures and at leisure to think about their breathing.

In addition, six experiments were done with subjects breathing oxygen. The minute volumes observed are not included in Fig. 7, but also fall within the same limits in all the experiments.

Tidal air. In Fig. 8 are plotted the tidal airs of two subjects (breathing air) against their oxygen consumption, with various intrapulmonary pressures

Through the results for each subject can be drawn a line, whose position is the same whatever intrapulmonary pressure is considered. It is clear that with these subjects there was no substantial change in tidal air with changes in intrapulmonary pressure.









Fig. 8. Effects of varying the intrapulmonary pressure on the tidal air at varying oxygen consumptions. E.P. =eupnoeic pressure.

This finding means that the frequency of respiration is also unchanged with changing intrapulmonary pressure.

There were indications that the tidal air is diminished on immersion as compared to that in air. Thus, no average tidal airs greater than 2 l. were observed even with the hardest work underwater—which is certainly not the case in air. But, owing to the variability of the tidal air in and between subjects, an extended comparison between conditions in air and water would be required. The change is evidently not a great one, since it is not enough to affect the minute volume.



Fig. 9. Manometer records of mouthpiece pressure. Subject working underwater at 220 kg.m./min. with minute volume = 27-30 l./min. A, eupnoeic pressure; B, eupnoeic pressure + 15 cm. water; C, eupnoeic pressure - 11 cm. water. Base-line corresponds to zero flow. Downward deflexion—inspiration; upward deflexion—expiration. Time signal 1 sec.



Fig. 10. Peak respiratory flow in subjects immersed in water at varying oxygen consumptions.

Response to CO_2 . The minute volume, when breathing 95% O_2 and 5% CO_2 in the horizontal and vertical positions, was compared with that out of water when lying down. No appreciable difference was found except when negative pressures were applied; there was then a considerable accentuation of the respiratory response.

Instantaneous respiratory flow. Despite the marked subjective differences experienced with varying intrapulmonary pressures, gross differences did not appear in the manometer recordings of mouthpiece pressure: no consistent alteration was detected in duration or amplitude of either inspiratory or expiratory phases. Specimen records are shown in Fig. 9. From the records, peak flows for each phase were obtained at various minute volumes, and are shown in Fig. 10.

DISCUSSION

The eupnoeic pressure

The original aim of this investigation—the discovery of the most suitable intrapulmonary pressure underwater-has been achieved. It is possible to define this 'eupnoeic' pressure with considerable accuracy, since it is readily distinguished and falls within fairly narrow limits for the group of subjects studied, i.e. 5–10 cm. below the ear in the upright position at rest, and at the supra-sternal notch for all other positions. Nevertheless, departures from the eupnoeic pressure, sufficient to produce discomfort, have surprisingly little effect on the character of the breathing in the steady state. They do not modify the frequency of respiration, the volume of tidal air or minute volume. They do not impair the response to CO_2 . They do not, by increasing the respiratory work, cause any substantial increase in oxygen consumption or produce any change in shape or amplitude of the respiratory cycle. There is an effect on the vital capacity and its components, but the effect does not seem to be functionally important. Thus, the selection of the eupnoeic pressure rests primarily on subjective criteria, and no means were found to define its limits on a basis of objective physiological activity. That is to say, the importance of eupnoeic pressure depends on the emphasis placed on the comfort of a diver.

If a bag cannot be designed so that the pressure of air respired shall be eupnoeic in all positions, or even in the usual position of the diver, there remains the question, in which direction is deviation preferable. There is no doubt that it should be in the positive direction, for the following reasons. Positive pressures were unanimously reported as preferable to negative pressures of equal magnitude. The experiments on respiratory resistance provided a crucial test; for, where a symmetrical resistance was imposed, it was found to be treated in the same way as an inspiratory one, the expiratory element in it being relatively ignored. Positive pressures increase the vital capacity underwater. Finally, positive pressures appear to be less dangerous than negative (cf. Stigler, 1911).

It should be observed, however, that this experimental work is reassuring in that no ill-effects, other than that of discomfort, followed sustained moderate deviations from eupnoeic conditions.

These considerations are relevant to submarine escape apparatus where a low position of the venting valve, and its appreciable resistance, together with the

high rate of venting, may cause a considerable and increasing positive pressure to develop during ascent. This pressure may be substantially greater than the positive pressures investigated by us. There is no doubt that such high pressures may be very dangerous (Polack & Adams, 1932). It must be stressed, therefore, that our conclusions as to the harmlessness of positive pressures apply only to the range studied, and to steady pressures within that range.

Vital capacity and reserve air

Before considering the theory of eupnoeic pressure, it is convenient to discuss the collapse of the thorax as shown by the diminution of the vital capacity and of the reserve air, due to immersion in water. Some of this effect is due to the fact that the weight of the viscera no longer affects the respiratory apparatus. Hamilton & Mayo (1944) found a diminution of 300 c.c. in the vital capacity following immersion to the nipple line. A similar effect occurs when the horizontal posture is assumed in air; McMichael & McGibbon (1939) found an average diminution of about 500 c.c. in the vital capacity and an average reduction of the reserve air from 1.7 to 1.0 l. when a subject changed from the sitting to the lying position. The diminution in vital capacity (730 c.c.) and the reduction in the reserve air (to 500 c.c.) following immersion are, however, greater than this.

The tendency of a perfectly elastic body filled with gas and submerged is to collapse at the base and to distend at the top. The upper portion of the thoracic cage, however, is relatively indistensible, whereas the lower portion is relatively collapsible. If therefore the lungs are in communication with a gas-reservoir, so that the volume of the thorax can change without alteration in the intrapulmonary pressure, the volume of the thorax must diminish, and to maintain it at its previous volume will require an extra inspiratory effort. It is therefore to be expected: (1) that the vital capacity will diminish on immersion, for work must be done against the water as well as against the usual resistances operating during maximal inspiration; (2) that the position of tidal respiration will shift towards expiration, for to maintain underwater the normal position at the end of an expiration will require an inspiratory effort. Unless, therefore, the end of expiration ceases to be a position of rest during immersion in water (which is not the case), we should anticipate a diminution of reserve air.

Pooling of venous blood in the thorax has been suggested as an element in the diminution in vital capacity following recumbency, and could equally well occur when the hydrostatic effects of the vertical posture are abolished by immersion in water. The results of experiments on the residual air leave this question open. It was found that residual air diminished by an amount varying from zero to 300 c.c. in various individuals. This slight diminution could be due to either or both of two causes: (a) the entry of an equivalent volume of blood into the thorax, the position of maximum expiration being

held unaltered by immersion; (b) accentuation of the position of maximum expiration on immersion, the blood content of the thorax remaining constant. (It is regarded as extremely unlikely that the position of maximum expiration should be relatively *expanded* by immersion, in view of the great diminution in reserve air.) Of these two possibilities, we favour the second, for two reasons: first, that the chest is known to be relatively collapsed, so that the effort of expiration is favoured by immersion: second, that if a shift of blood were occurring, one would expect it to occur in all subjects, rather than in only three out of five; whereas such irregularity is only to be expected where a muscular effort is concerned. Whatever the explanation, the diminution in residual air is small, and even assuming it all to be due to venous pooling, the bulk of the diminution in vital capacity found on immersion must be ascribed to other causes.

Theory of eupnoeic pressure

The main part of the following discussion refers to a diver at rest or doing light work in the vertical head-up position.

The salient point about the eupnoeic pressure is that it corresponds to a pressure of water at a level above the highest point of the lungs. It might reasonably have been supposed that it would correspond to a point somewhere about the middle of the thorax. This may be stated more rigorously as follows:

Assuming for the moment a thorax of uniform collapsibility, consider what pressure (P) should exist inside the thorax, so that the efforts of inspiration and expiration should be equal. If P = pressure of water at the level of the base of the lungs, it will be easy to inspire, but hard to expire; if P = pressure of water at the level of the top of the head, it will be hard to inspire, but easy to expire; for intermediate values of P, the resultant forces will tend to collapse the bases and expand the apices of the lungs in varying degrees. What is required is a pressure such that this collapse and expansion will balance, so that there is no *resultant* distending or compressing force; i.e. a pressure which, evenly diffused over the inside of the thorax, is just equal to the sum of the pressure gradient on the outside in an immersed subject. This pressure is familiar in mechanics as the pressure at the level of the 'centre of pressure' (or 'centroid'), a point in general slightly lower than the centre of buoyancy. There are no data as to the position of the centre of buoyancy of the chest, but it is certainly below the point half-way between supra-sternal notch and xiphoid process, and the centre of pressure is a fortiori at least 25 cm. below the ear, probably more.

These considerations show that an explanation is required as to why the 'expected' eupnoeic pressure is substantially greater than the experimentally determined eupnoeic pressure. It might be supposed that the basis of the sensation of eupnoeic depth is a compromise between the sensations experienced

throughout the respiratory tract, from the mouth to the base of the lungs, so that the pressure chosen is such that the sensations of inflation and deflation over the whole depth of the respiratory tract balance each other as far as possible. This implies of course, that a relatively negative pressure is tolerated by the chest and a relatively positive one by the mouth. The final pressure chosen would be expected to be about the mid-point of the whole tract, which is not far from the point determined by experiments.

There is no doubt (from subjects' reports) that mouth sensation plays a part in determining selection of eupnoeic pressure in some cases. There are, on the other hand, some subjects who definitely decide purely by thoracic sensation, and to whom this theory of sensory compromise seems inapplicable. A further difficulty is that the theory supposes a substantial negative pressure to be tolerated by the chest, as part of the compromise with the mouth; there is no such sensation experienced at eupnoeic pressure, and it is one that anybody underwater avoids, positive pressure being much preferable. It is possible that a small negative pressure is tolerated at rest, but not when working; this would contribute towards the lowering of eupnoeic pressure during hyperpnoea.

An alternative theory may be advanced, depending on the thoracic collapse discussed above. Two factors enter from this cause which will tend respectively to raise the centre of pressure and to make inspiration easier, thus lessening the expected eupnoeic pressure. The first of these is that the collapse of the base of the thorax by immersion must at once raise the centre of pressure by a small amount, simply because the dimensions of the thoracic cavity are now smaller in the downward direction.

The second factor is somewhat complicated. The normal respiratory resting position of the chest depends on the balance between the inward elastic recoil of the lungs and the outward spring of the thoracic cage (a composite force involving the ribs, diaphragm, viscera and abdominal wall). Thus an equation of forces acting in opposite directions on the thoracic wall may be written: (intrapulmonary pressure) + (intrapleural pressure) = (average external thoracic)pressure) - (outward spring of thoracic cage); intrapleural pressure is, of course, usually negative, and is equal and opposed to the thoracic outward spring. When the subject is immersed, the intrapulmonary pressure represents the eupnoeic pressure, and the average external thoracic pressure is equivalent to the pressure at the centroid. So far as immersion merely abolishes the effect of the weight of the viscera, the equality of eupnoeic pressure and centroid pressure is not disturbed, since the thoracic cage collapses a little, and intrapleural pressure is still equal and opposite to the thoracic outward spring. But the thoracic cage is collapsed further than this, as discussed above, due to its being an air-containing cavity with a relatively rigid upper part and collapsible lower part. This compression of the thorax both increases the thoracic outward

spring, and increases the intrapleural pressure (i.e. lessens its negativity), so that they cease to be equal in magnitude. Accordingly the eupnoeic pressure can no longer equal the centroid pressure but must be less, by the sum of the amounts by which the intrapleural pressure and the thoracic outward spring are each increased. The magnitude of this sum is uncertain, but can be estimated (from known variations in intrapleural pressure) as of the order of 10 cm. of water. The eupnoeic pressure then approaches the value found experimentally. (This analysis is necessarily tentative, in the absence of data on intrapleural pressure underwater, and on the magnitude of the thoracic elasticity with varying distension of the thorax.)

The above explanation is essentially in terms of the sensation of muscular effort in breathing underwater, which is desirable, since it is mostly by the balancing of inspiratory and expiratory effort that the eupnoeic choice is made, and since muscular activity is capable of the fine and continuous discrimination observed. What the ultimate sense-receptors are is not clear; probably the proprioceptors of respiratory muscle are most concerned. But other sets of receptors exist in the pulmonary field, and it is of interest that the eupnoeic level is not very far from that of the pulmonary venous pressure in the chest when not immersed; the possibility arises that afferents from pulmonary veins may transmit nerve impulses when there is deviation from eupnoeic pressure. Such nerve impulses may be responsible for the unpleasantness of negative pressures (when the veins would be distended) as compared with positive pressures (when they would be collapsed).

In positions other than the head-up. In horizontal positions, it is clear that the pressure gradient of water against the thorax is nearly abolished, so that the factors described above do not operate. We should expect the eupnoeic pressure to be about the level of the centre of pressure—i.e. a little below the centre of buoyancy—which agrees with our findings.

In the vertical, head-down position, we should expect the thorax to become distended since the distensible part of the thorax is now uppermost. This distension adds a certain volume to the upper part of the thorax, raising its centre of pressure; but at the same time the balance of forces is disturbed in the opposite direction to those previously described, so that the eupnoeic pressure must exceed the centroid pressure. Thus the eupnoeic pressure should be in the same position on the body as regards thoracic balance of forces, but the factor of dimension-change acts in the opposite direction. We should expect, therefore, that the eupnoeic pressure should now be nearer the supra-sternal notch and farther from the ear than it was in the erect posture. This, within the limits of the few experiments done, was found to be so.

The increase of eupnoeic pressure with hyperphoea, in the erect position, is probably due to two factors; one, mentioned above, that a certain small negative pressure required for mouth comfort is no longer tolerated; the other,

that the subject wishing to be quite certain that he will not experience inspiratory resistance, chooses as eupnoeic pressure, a pressure with a slight expiratory resistance.

SUMMARY

1. Experiments have been made to find the most comfortable pressure of the respired air (eupnoeic pressure) when a subject is immersed. The effect of immersion on the vital capacity, on reserve, complemental and residual airs, minute volume, on tidal air and on the form of the respiratory cycle at various intrapulmonary pressures and grades of work were also studied.

2. The eupnoeic pressure is 5-10 cm. below the external auditory meatus in the erect position at rest, increasing to 10-15 cm. when there is hyperphoea from any cause. In all positions other than the erect, eupnoeic pressure is at the level of the supra-sternal notch.

3. The vital capacity is reduced during vertical immersion, is further reduced by negative intrapulmonary pressures and is partially restored by positive pressures.

4. The reserve air is diminished during vertical immersion at eupnoeic pressure, with a corresponding increase in complemental air. In the horizontal position, at eupnoeic pressure, the volumes of reserve and of complemental air are similar to those in air. The residual air is slightly diminished by immersion vertically.

5. Deviations up to 15 cm. less, or 20 cm. greater, than eupnoeic pressure are without effect on minute volume, on tidal air and on the shape of the respiratory cycle in the steady state.

6. The origin of the eupnoeic pressure and its relation to the partial collapse of the thoracic cavity following immersion are discussed.

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